RESEARCH ARTICLE

American Journal of Botany

What makes a weed a weed? A large-scale evaluation of arable weeds through a functional lens

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Manuscript received 6 July 2018; revision accepted 1 November 2018.

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Citation: Bourgeois, B., F. Munoz, G. Fried, L. Mahaut, L. Armengot, P. Denelle, J. Storkey, et al. 2019. What makes a weed a weed? A large-scale evaluation of arable weeds through a functional lens. *American Journal of Botany* 106(1): 90–100.

doi:10.1002/ajb2.1213

PREMISE OF THE STUDY: Despite long-term research efforts, a comprehensive perspective on the ecological and functional properties determining plant weediness is still lacking. We investigated here key functional attributes of arable weeds compared to non-weed plants, at large spatial scale.

METHODS: We used an intensive survey of plant communities in cultivated and non-cultivated habitats to define a pool of plants occurring in arable fields (weeds) and one of plants occurring only in open non-arable habitats (non-weeds) in France. We compared the two pools based on nine functional traits and three functional spaces (LHS, reproductive and resource requirement hypervolumes). Within the weed pool, we quantified the trait variation of weeds along a continuum of specialization to arable fields.

KEY RESULTS: Weeds were mostly therophytes and had higher specific leaf area, earlier and longer flowering, and higher affinity for nutrient-rich, sunny and dry environments compared to non-weeds, although functional spaces of weeds and non-weeds largely overlapped. When fidelity to arable fields increased, the spectrum of weed ecological strategies decreased as did the overlap with non-weeds, especially for the resource requirement hypervolume.

CONCLUSIONS: Arable weeds constitute a delimited pool defined by a trait syndrome providing tolerance to the ecological filters of arable fields (notably, regular soil disturbances and fertilization). The identification of such a syndrome is of great interest to predict the weedy potential of newly established alien plants. An important reservoir of plants may also become weeds after changes in agricultural practices, considering the large overlap between weeds and non-weeds.

KEY WORDS agroecosystems; ecological strategies; environmental filtering; farmland biodiversity; hypervolume; intensive agricultural practices; plant functional niches; trait-based approach; weed fidelity index; weediness syndrome.

Weeds are classically defined as plants that spontaneously grow on a land modified by humans (Godinho, 1984), while arable weeds are those specifically occurring in regularly cultivated fields. Despite several efforts to define weediness in ecological terms (Baker, 1965; Sutherland, 2004; van Kleunen et al., 2010; Kuester et al., 2014), there is still no definite answer to the question "What makes a weed a weed?" One may therefore question whether arable weeds represent an artificial construct without clear ecological identity defined purely on the basis of plant presence in arable fields, or conversely, consist of an ecologically meaningful pool of plants characterized by specific adaptations to arable fields. In this context, trait-based ecology provides a relevant approach to assess the characteristics and determinants of the ecological niche of arable weeds (Grime, 1974; Westoby and Wright, 2006). Ecological niche differentiation along multiple functional dimensions indeed drives plant adaptation to specific environmental conditions and results in basic ecological strategies (Grime, 1979; Blonder et al., 2014, 2017). Our aim was to characterize whether and how the niche of arable weeds is constrained by specific trait values related to resource requirement, competitive ability, phenology, and resistance to disturbance that confer adaptation to the specific environment of arable fields.

Defining a reference pool of arable weeds is challenging since a very broad diversity of definitions of weeds has been proposed, thereby evidencing that no consensus has yet been reached to define these organisms (see e.g., the 13 definitions of weeds cited by Zimdahl, 2013). In addition, arable weeds represent a melting pot of species with different biogeographic and ecological backgrounds (Baker, 1974; Munoz et al., 2017). In Europe, some arable weeds are native to open natural habitats, e.g., riparian zones or dry grasslands, which act as potential sources of species in current agroecosystems (Jauzein, 1995). Other species, conversely, did not exist naturally in European habitats and have been accidentally introduced with crop seeds (Coward et al., 2008). Some of these introduced arable weeds, so-called archaeophytes, have occurred in crops since the beginning of agriculture (~10,000 BP) and are absent in natural habitats today, even in areas of cereal domestication. Over a long period, agriculture practices may have selected highly adapted ecotypes mimicking crop phenology and morphology (Neve et al., 2009). Arable weeds thus include both species present in arable fields and open non-arable habitats (e.g., *Galium aparine*, *Lapsana communis*) and species confined to arable fields, so-called messicoles (i.e., arable weeds specialized to winter cereal fields such as *Agrostemma githago* and *Bupleurum rotundifolium*; Fried et al., 2010). Arable fields, therefore, represent both an extended niche for generalist or pre-adapted species, and a specific niche for a specialist flora selected for by agronomic constraints (Vigueira et al., 2013).

Previous studies investigated weediness either by focusing on small sets of locally co-occurring species or challenging lists of weeds and non-weeds using broad definitions (i.e., including non-arable invasive species as weeds: Sutherland et al., 2004; Kuester et al., 2014), potentially missing ecological contrasts that are specific to the context of arable fields. Furthermore, trait-based analyses have to date been limited by a lack of data on all but commonly recorded traits. However, growing efforts to compile databases on traits and vegetation worldwide (e.g., Violle et al., 2014) now allow more comprehensive and quantitative assessments of arable weed functional attributes at a large spatial scale. A comparative approach of arable weed trait values against those of plants restricted to open non-arable habitats should shed a new light on the ecological identity of arable weeds. Arable weeds can thus differ from non-weeds by (1) moderate functional differences, so that almost all species of surrounding habitats can disperse in an arable field and become arable weeds, or by (2) large functional differences representing adaptations to specific environmental constraints in arable fields, which should limit exchanges with surrounding habitats and help to predict the weedy potential.

Agricultural management results in harsh environmental constraints making arable fields a challenging habitat for plants. Arable fields are exposed to regular disturbances from tillage and weeding, high nutrient availability due to fertilization, and important temporal heterogeneity related to crop sequences (Gaba et al., 2014). Crop dominance also leads to high competitive pressure for resources including space and light (Weiner, 1990; Perry et al., 2003). We expect arable weeds will be characterized by specific traits promoting persistence under these conditions. The leaf–height–seed scheme (LHS; Westoby, 1998) has proved particularly successful in describing the main functional dimensions driving plant responses to environmental constraints, namely, the ability to grow, compete, reproduce, and disperse (Díaz et al., 2016). Few studies, however, have tested this scheme in cultivated contexts (Storkey, 2006; Fried et al., 2012; Perronne et al., 2015). In addition to selecting for LHS traits, farming operations timing and frequency together with soil disturbances intensity should select phenological traits and life-form, respectively (Baker, 1974; Zanin et al., 1997; Gaba et al., 2017). High nutrient and low light availabilities may additionally filter arable weeds depending on resource-use strategy and stress tolerance. Such constraints could have led to large differences in species affinity for arable fields within the arable weed flora: some weeds are frequent in arable fields and others rare. Assessing arable weed trait variations along such a specialization gradient should help understand the ecological processes determining weed performance in arable fields. Overall, one may expect arable weeds, notably weeds with high specialization to arable fields, to occupy a restricted subset of the global functional trait space of plants (Díaz et al., 2016).

In this study, we aimed to characterize the functional nature of arable weeds by comparing the functional trait values of arable weeds against those of non-weeds over a large geographical area with broad environmental variations. An index of specialization to arable fields was then calculated based on an intensive survey of weed occurrences in arable fields and in other habitats. We then analyzed functional variation along a gradient of weed fidelity to arable fields. Species pools were compared for nine traits separately and for three functional spaces (i.e., sets of traits) representing LHS, reproductive, or resource requirement strategies, respectively. We used a hypervolume approach to compute the geometry of multidimensional niches (Blonder et al., 2014, 2017). We expected a distinct and narrower spectrum of ecological strategies among arable weeds compared to non-weeds and within weeds with higher fidelity to arable fields compared to weeds with lower fidelity. Based on the differences among pools, we discuss arable weed functional specificities in relation to the ecological mechanisms likely to promote persistence in arable fields.

MATERIALS AND METHODS

Delineation of arable weed and non-weed species pools

Several flora and field inventories conducted over France were compiled to exhaustively delineate a pool of arable weed species, and a pool of non-weed species. First, the list of species occurring in arable fields (Munoz et al., 2017) included species retrieved from (1) a comprehensive specialized flora of arable fields (Jauzein, 1995), (2) the Biovigilance-Flore Network that sampled 1440 arable fields across France during 9 years (Fried et al., 2008), (3) a survey of 3000 arable fields over 10 years in the LTSER Zone Atelier “Plaine & Val de Sèvre” (a 450-km² intensive farmland landscape of western France; Bretagnolle et al., 2018), and (4) the governmental reference list of messicole species (Cambecèdes et al., 2012) to account for Red-Listed arable weeds generally not detected in field surveys. Second, a list of plants occurring in open non-arable habitats was obtained from the Divgrass database (Violle et al., 2015), which encompassed 51,486 vegetation plots over France for a total of 5245 species. These open non-arable habitats corresponded to surveys of permanent grasslands (see Violle et al., 2015 for further details). The Divgrass database further assigned habitat types to each species based on a global co-occurrence analysis (i.e., modularity analysis), yielding basic vegetation categories (Carboni et al., 2016). Species present in both arable fields and open non-arable habitats mainly belonged to four types of permanent grasslands: (1) dry calcareous grasslands, (2) mesic grasslands, (3) ruderal and trampled grasslands, and (4) mesophilous and nitrophilous fringes. We thus compared arable weeds and non-weeds from these four basic habitats, thereby excluding species specific to mountainous grasslands or wetlands for example. Therophytes, hemicryptophytes, and geophytes only were considered to therefore focus on non-climbing herbaceous species.

Species were finally classified into two pools: (1) plants inventoried in both arable fields and open non-arable habitats (hereafter, arable weeds; 1383 species), and (2) plants inventoried only in open non-arable habitats (hereafter, non-weeds; 998 species). Interestingly, 13 plants listed as invasive aliens in France (Gargominy et al., 2017) were present in the weed species pool [*Ambrosia artemisiifolia* L., *Artemisia verlotiorum* Lamotte, *Bidens frondosa* L., *Bromus catharticus* Vahl,, *Dysphania ambrosioides* (L.) Mosyakin & Clemants, *Helianthus tuberosus* L., *Impatiens glandulifera* Royle, *Paspalum dilatatum* Poir., *Paspalum distichum* L., *Reynoutria japonica* Houtt., *Solidago canadensis* L., *Solidago gigantea* Aiton, and *Sporobolus indicus* (L.) R.Br.], while only one was present in the non-weed pool (*Cortaderia selloana* (Schult. & Schult.f.) Asch. & Graebn).

Functional trait data

We characterized plant ecological strategies using nine functional traits (Table 1). The LHS scheme (Westoby, 1998) was represented by plant height, seed mass, and specific leaf area (SLA). We assessed phenology and reproductive strategies through flowering onset and flowering duration (in months; flowering duration refers to the flowering period for a species, not an individual). Raunkiaer biological types represented varying responses to stress and disturbances, and we assessed species resource requirements based on Ellenberg indices for nitrogen, light, and moisture (Ellenberg et al., 1992). The six latter traits were extracted from the Baseflor database (Julve, 1998), whereas the three LHS traits were obtained from the BiolFlor (Klotz et al., 2002), Ecoflora (Fitter and Peat, 1994), and LEDA databases (Kleyer et al., 2008).

Statistical analyses

First, functional differences between arable weeds and non-weeds were investigated by comparing each trait distribution separately between the two pools. For LHS traits, we permuted trait values between pools (pool sizes kept constant) and calculated functional overlap, measured as the area common to both trait distributions (in %), under a null hypothesis of no functional difference between pools (Perronne et al., 2014). We simulated 1000 null overlap values and compared them to the observed overlap with actual species trait values, with a significance threshold of 0.05. For the other six (non-quantitative) traits, we assessed differences in trait distributions between arable weeds and non-weeds by performing χ^2 tests.

Second, we compared the hypervolumes of arable weeds and non-weeds in multidimensional functional space. The hypervolume method uses threshold kernel density estimation to calculate a multidimensional volume approximating the functional space occupied by a set of species, while acknowledging the presence of holes and potential outliers (Blonder et al., 2014, 2017). Three types of hypervolumes were considered here: (1) one based on LHS traits (SLA, plant height, and seed mass), (2) one relying to reproductive strategies (based on flowering onset, flowering duration, and seed mass), and (3) one related to resource requirements (calculated from Ellenberg indices for nitrogen, light, and moisture). We thus considered three types of hypervolumes rather than a single one to separate the contributions of specific components of the global plant strategies (LHS, reproduction, or resources) to the differentiation between arable weeds and non-weeds. To control for different numbers of species in each pool, we applied a rarefaction approach: *n* arable weed species were subsampled 1000 times, with *n* corresponding to the number of non-weed species (the smallest species pool). Therefore, 1000 arable weed hypervolumes and one non-weed hypervolume were calculated for each of the three types of hypervolumes. Differences in functional niche breadth between arable weeds and non-weeds were tested by calculating the *p*-value between the frequency distribution of the 1000 hypervolume volumes of arable weeds and the non–weed hypervolume volume. A *p*-value value inferior to 0.025 or superior to 0.975 indicates a non-weed hypervolume significantly smaller or larger than the arable weed hypervolume, respectively. In addition, functional space overlap between arable weeds and non-weeds was assessed by calculating the number of arable weeds included in the non-weed hypervolumes.

The pool of arable weeds could include some species occasionally observed within arable fields and more frequently encountered in other habitats. To differentiate these occasional arable weeds and to derive a continuous metric of weediness, we assigned each arable weed species an index of fidelity to arable fields. We then assessed functional trait and hypervolume variations for varying levels of fidelity. These analyses only included plant species inventoried in the

TABLE 1. Description of investigated plant traits, obtained from the Baseflor, BiolFlor, Ecoflora and LEDA databases. Range corresponds to mean [min-max] for leaf–height–seed (LHS) traits (i.e., SLA, height and seed mass), and to median [min-max] for the others.

Trait	Type	Unit	Range / Level	No. of weed species informed (total: 1383)	No. of non-weed species informed (total: 998)
Specific leaf area	Quantitative (numeric)	$m^2\ kg^{-1}$	24.49 [3.48–71.27]	579	296
Plant height	Quantitative (numeric)	m	0.50 [0.01–2.74]	732	403
Seed mass	Quantitative (numeric)	g	4.19 [0.0008–99.17]	800	383
Biological type	Qualitative (factor)	—	therophyte – hemicryptophyte - geophyte	1365	968
Flowering onset	Quantitative (integer)	month	5 [1–12]	948	672
Flowering duration	Quantitative (integer)	month	7 [1–12]	948	672
Ellenberg nitrogen	Semi-quantitative (integer)	—	6 [1–9]	1022	707
Ellenberg light	Semi-quantitative (integer)	—	8 [1–9]	1025	719
Ellenberg moisture	Semi-quantitative (integer)	—	7 [1–11]	1015	703

Biovigilance-Flore Network (for a total of 289 species; Appendix S1), as this data set was the only one for which fidelity at a national scale could be calculated. Fidelity to arable fields in Biovigilance-Flore relative to open non-arable habitats in Divgrass was calculated for each species *i* using the *Φ* index proposed by Chytrý et al. (2002):

$$\Phi_i = \frac{N n_{i,\mathrm{p}} - n_i N_\mathrm{p}}{\sqrt{n_i N_\mathrm{p}\left(N - n_i\right)\left(N - N_\mathrm{p}\right)}}, \Phi_i \in [-1;1],$$

where N is the total number of surveys in both Biovigilance-Flore and Divgrass databases, N_p is the total number of surveys in Biovigilance-Flore, n_i is the number of occurrences of species *i* in both Biovigilance-Flore and Divgrass databases, and $n_{i,\mathrm{p}}$ is the number of occurrences of species *i* in Biovigilance-Flore. Higher fidelity index to arable fields therefore corresponded to species that occurred in a high number of plots in the Biovigilance-Flore database and a low number of plots in the Divgrass database, while lower fidelity index to arable fields corresponded to species that occurred in a low number of plots in the Biovigilance-Flore database and a high number of plots in the Divgrass database. Besides relative frequency, fidelity index correlates positively with the noxiousness of arable weeds as a preliminary analyses showed that arable weeds classified as noxious over France in the reference list proposed by Mamarot and Rodriguez (2011; Appendix S1) had a significantly higher fidelity to arable fields compared to arable weeds not classified as noxious (Appendix S2). Hence, the index of weed fidelity to arable fields represents a relevant proxy for weed noxiousness. Species were then sorted by decreasing fidelity to arable fields and split into nine subsets corresponding to fidelity deciles (i.e., the first decile included the species with the highest 10% *Φ* index, etc.). We assessed changes in the mean and variance of each of the nine traits across these subsets. While variations in mean trait values identified the direction of functional changes among arable weeds with increasing fidelity, we also investigated changes in trait variance to test whether the spectrum of ecological strategies was narrowing with increasing fidelity. Compared to classical linear models (i.e., analyzing fidelity index as a continuous variable), this approach based on fidelity deciles thus allowed us to quantify changes in single trait variance in comparison with random species pools. Narrower variance was expected if arable weeds with the highest fidelity were selected according to a specific set of functional attributes. For each trait and each of the nine decile subsets, we therefore calculated the observed variance and a series of null variances obtained from 1000 subsamples of k_i species randomly selected among all arable weeds, k_i corresponding to the number of species in subset *i*, with *i* in [1;9]. *P*-values of observed variance were then calculated as:

$$P = \frac{\sum(\text{null values} < \textit{obs. value}) + \frac{\sum(\text{null values} = \text{obs. value})}{2}}{n_\mathrm{perm} + 1},$$

where the null values are the variance values obtained from resampling, the obs. value is the observed variance, and n_perm is the number of permutations (1000). For each species subset *i*, a *P*-value lower than 0.025 or greater than 0.975 indicates a trait variance significantly smaller or higher than expected by chance, respectively.

We then examined the relationship between functional niche breadth and arable weed fidelity. As for trait variance, we expected hypervolume to become narrower when fidelity increases. We designed a comparable rarefaction procedure to test the deviation of each of the three hypervolumes from null volumes along a gradient of fidelity. This null model approach indeed allowed us to account for differences in species richness between fidelity deciles and thus avoid potential biases as hypervolumes calculated with fixed bandwidth necessarily increase with species richness (Lamanna et al., 2014). Last, we assessed changes in the difference between arable weed and non-weed functional spaces along a gradient of fidelity by computing the distance between the centroids of arable weed and non-weed hypervolumes for each fidelity decile and each type of hypervolume (total of 27 distances).

Analyses were conducted in R v.3.2.3 (R Core Team, 2016) using the package hypervolume (Blonder and Harris, 2017). We did not consider plant taxa for which the trait value was not available in single trait comparisons (Table 1) or plant taxa missing at least one value among investigated traits in hypervolume computation (see figure legends).

RESULTS

Differences in functional traits between arable weeds and non-weeds

We found significant differences between arable weeds and non-weeds for most functional traits (Fig. 1; Appendix S3). Regarding LHS traits, arable weeds generally tended to have a higher SLA than non-weeds, whereas plant height and seed mass did not differ significantly between arable weeds and non-weeds. Regarding Raunkiaer biological types, arable weed species included more than 60% of therophytes, while non-weeds were mainly hemicryptophytes and geophytes (65% and 20%, respectively). In terms of flowering phenology, arable weeds generally started to flower earlier (in March and April) and approximately 25% of the weeds flowered longer than the non-weeds (up to 9–10 months; Fig. 1; Appendix S3). Regarding Ellenberg indices, arable weeds had a higher affinity for nitrogen-rich soils, sunnier environments and drier conditions compared to non-weeds (Fig. 1; Appendix S3).

Differences in functional spaces between arable weeds and non-weeds

Functional spaces differed between arable weeds and non-weeds for two of the three hypervolumes studied. Arable weeds were characterized by a smaller LHS hypervolume than non-weeds (mean arable weed $_\text{LHS vol}$ ± SD = 65 ± 5; non-weed $_\text{LHS vol}$ = 107; $p_\text{LHS vol difference} < 0.0001$; Fig. 2A; Appendix S4a), as well as a smaller resource requirement hypervolume (mean arable weed $_\text{resource vol}$ ± SD = 44 ± 2; non-weed $_\text{resource vol}$ = 71; $p_\text{resource vol difference} < 0.0001$; Fig. 2B; Appendix S4b), reflecting a narrower niche space of arable weeds. Despite these differences, large overlap in functional niches were found between the two pools, as up to 97% and 94% of the arable weeds were included in LHS and resource requirement hypervolumes of non-weeds, respectively. Only hypervolumes related to reproductive strategies showed no significant volume differences between arable

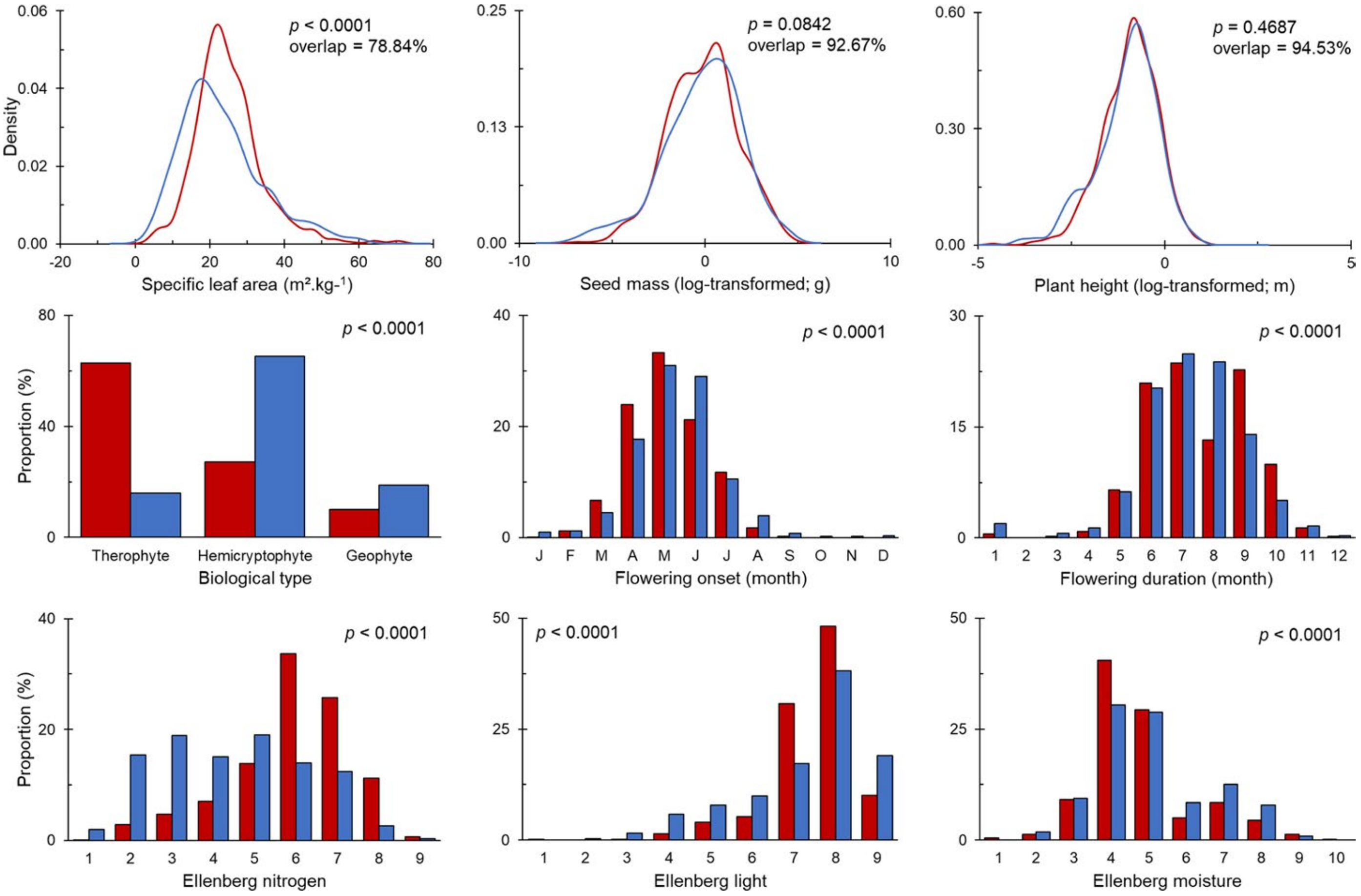

FIGURE 1. Distribution of plant traits among the two species pools (red: arable weeds; blue: non-weeds). The *p*-values for between-pool differences in trait distribution were obtained from a null model approach for leaf–height–seed traits and χ^2 tests for the others. Species pool size is indicated in Table 1, and detailed results of the χ^2 tests in Appendix S3.

weeds and non-weeds (mean arable weed $_{\text{reproductive vol}}$ ± SD = 65 ± 4; non-weed $_{\text{reproductive vol}}$ = 61; p $_{\text{reproductive vol difference}}$ = 0.1822; Fig. 2C; Appendix S4c); more than 90% of the arable weeds were included in the non-weed hypervolume (mean inclusion calculated from the 1000 species subsamples).

Variation in arable weed functional traits with increasing fidelity to arable fields

We found significant changes in mean functional trait values with increasing arable weed fidelity to arable fields (Appendix S5): SLA, flowering duration, and Ellenberg index for nitrogen increased on average, while Ellenberg index for light and flowering onset decreased. Species more confined to arable fields thus flowered earlier, produced flowers over a longer period, and had higher affinity for nitrogen-rich soils and shady environments. For Ellenberg index for moisture, a gradual decrease was followed by an increase after the 30% decile with increasing fidelity. The proportion of therophytes also increased with arable weed fidelity, while the proportion of hemicryptophytes decreased (Appendix S5). Conversely, the mean of plant height and seed mass did not vary significantly along the fidelity gradient.

The variance of Ellenberg indices for nitrogen, light, and moisture decreased with increasing fidelity to arable fields and rapidly became lower than expected for random subsamples of the same size from the entire arable weed pool (Fig. 3). A narrower range of resource requirements strategies thereby characterized arable weed species with higher fidelity to arable fields. Conversely, for the other traits, decreases in trait variance with increasing fidelity were not significant (Fig. 3), suggesting that diverse LHS and reproductive ecological strategies facilitate the colonization of arable fields.

Variations in arable weed functional spaces with increasing fidelity to arable fields

We assessed hypervolume variations along the arable weed fidelity gradient. Only the resource requirement hypervolume (i.e., based on Ellenberg indices) showed a volume that rapidly dropped and became significantly smaller than expected from random subsamples of same size among the entire arable weed pool (Fig. 4; Appendix S6). Along the fidelity gradient, arable weeds thus experienced important narrowing in the breadth of their functional niche related to abiotic requirements, given that only a limited number of combinations of Ellenberg indices characterized arable weeds with higher affinity to arable fields. Hence, the volume of resource requirement hypervolume decreased by 80% when the 10% of the arable weeds with the highest fidelity to arable fields was compared to the entire pool was, and by 37% and 17% for LHS and reproductive

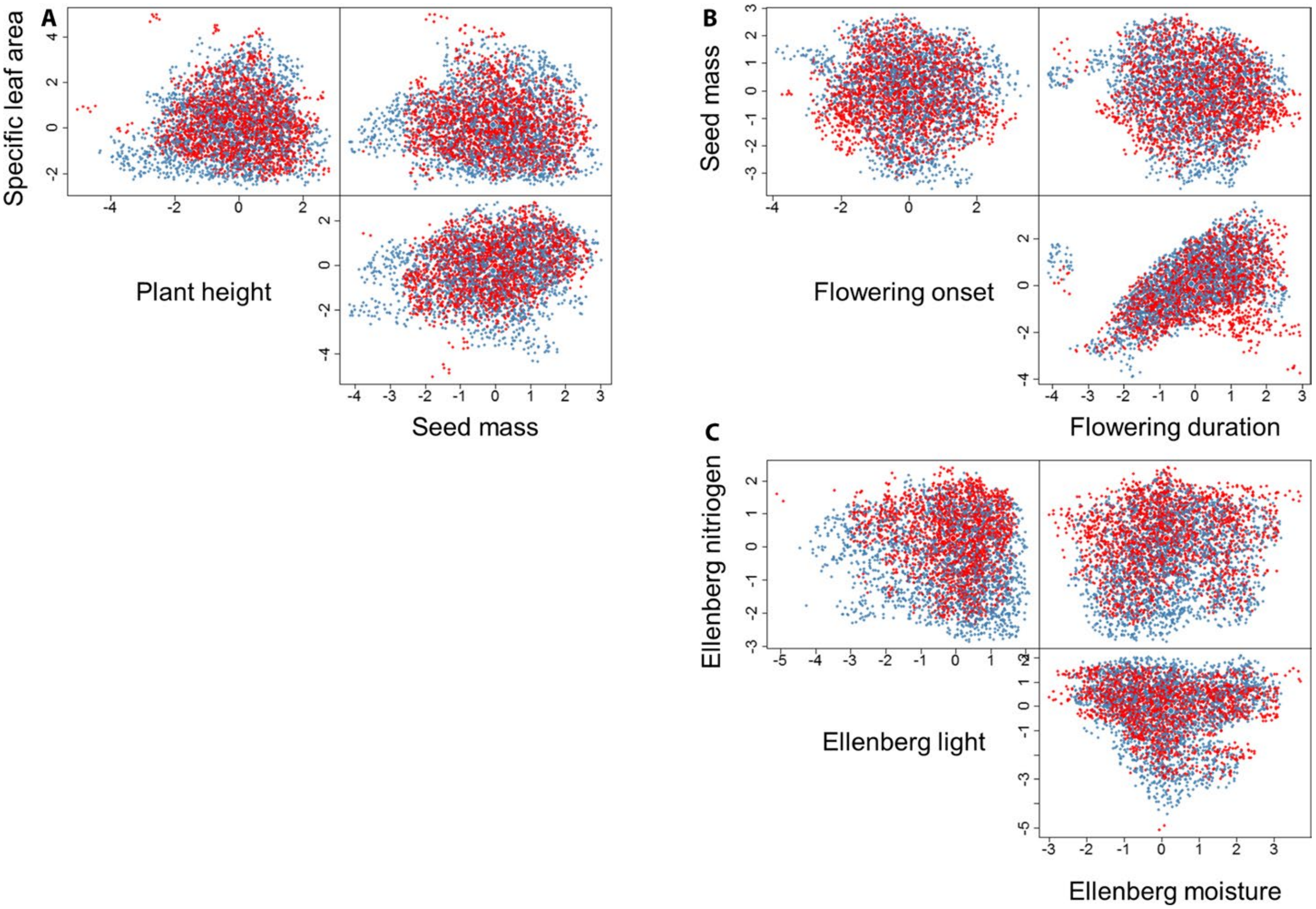

FIGURE 2. Pairwise representation of the arable weed (red) and non-weed (blue) hypervolumes based on (A) leaf–height–seed traits (n = 524 species), (B) reproductive traits (n = 550 species), and (C) resource requirement indices (n = 1406 species). Only one of the 1000 hypervolumes calculated by resampling is shown for arable weed species.

hypervolumes, respectively. Although the volumes of the LHS and reproductive hypervolumes decreased along the gradient of fidelity, these hypervolumes were not significantly smaller than expected by chance from random species samples (null hypothesis) even for the 10% of arable weeds with the highest fidelity to arable fields. Furthermore, the distance between the centroids of the arable weed and the non-weed hypervolumes positively increased with fidelity for the three types of functional spaces, indicating greater functional discrepancy between arable weeds with the highest fidelity to arable fields and the non-weed species (Appendix S7).

DISCUSSION

Characterizing the functional space of species occurring in a specific habitat allows better understanding of the ecological mechanisms driving their persistence and coexistence (McGill et al., 2006; Blonder et al., 2014). Here, we investigated the functional specificities of arable weeds (1) compared to plants found in non-arable open habitats (non-weeds) and (2) along a gradient of fidelity to arable fields. We used two complementary approaches: single-trait and multidimensional functional space comparisons, which provide complementary insights into basic ecological strategies (Díaz et al., 2016). We found that arable weeds, especially those with high fidelity to arable fields, are characterized by key trait values promoting their persistence under the harsh constraints imposed by agricultural management. Nevertheless, the functional niches of arable weeds and non-weeds broadly overlapped, so that most arable weeds were included in non-weed hypervolumes. The functional difference still increased between non-weeds and the arable weeds with the highest fidelity to arable fields, thereby demonstrating that the concept of weediness is best interpreted as a continuum of specialization as opposed to a discrete categorization.

Ecological filters driving arable weed functional specificities

Arable weeds with highest fidelity to arable fields are characterized by higher specific leaf area and a low Ellenberg index for light reflecting their ability to better acquire resources while tolerating competition for light with crops, one of the main limiting resources in arable fields (Weiner et al., 2010). Higher specific leaf area can be indicative of a large growth potential when resource availability is high, in accord with previous studies defining two types of weed strategies: tall, fast-growing species running for light acquisition

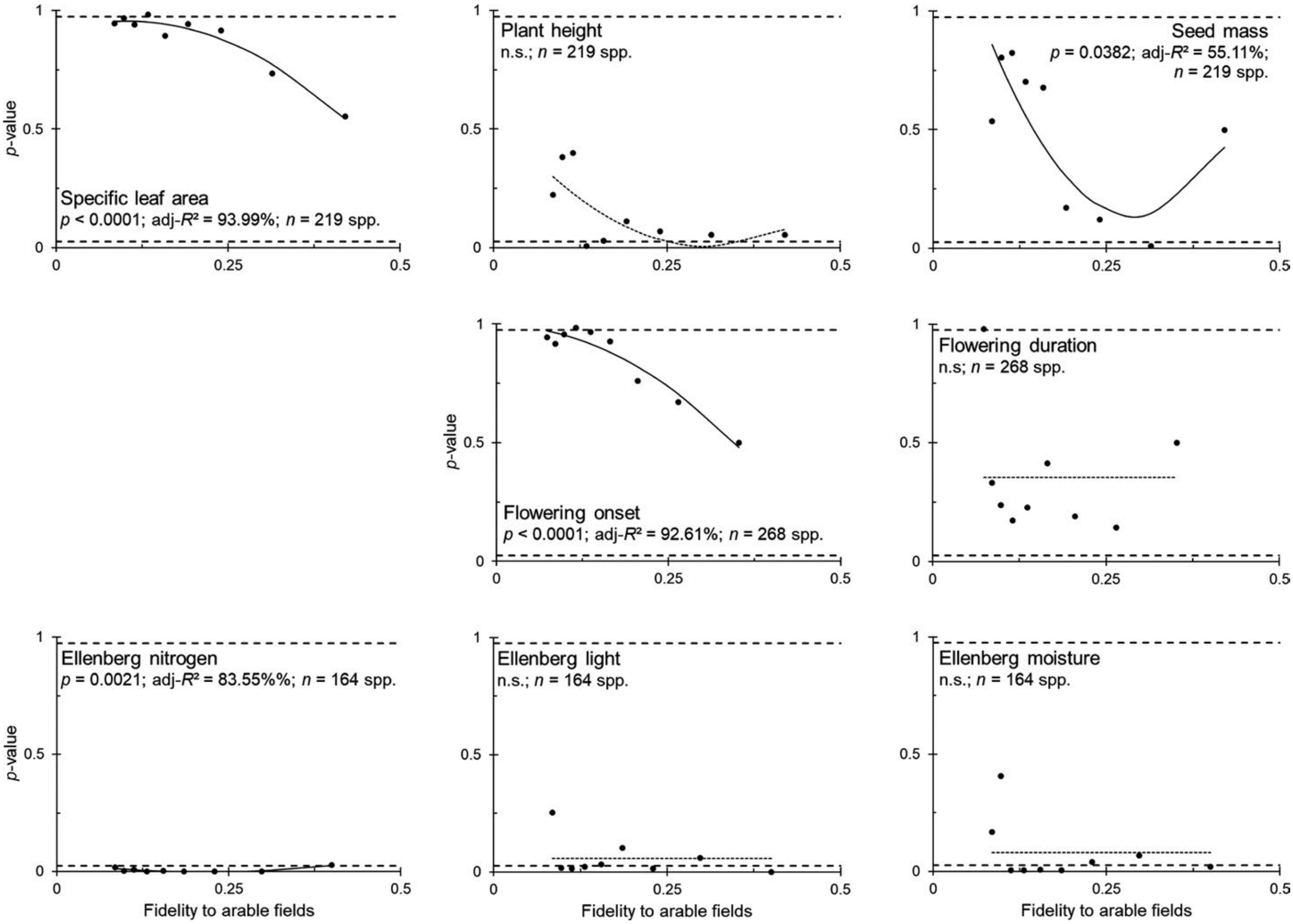

FIGURE 3. Variation in the p-value of the investigated trait variance along a gradient of arable weed species fidelity to arable fields. The p-values obtained through resampling correspond to the probability of trait variance to be significantly smaller ($p \leq 0.025$) or higher ($p \geq 0.975$) than expected by chance (dotted lines show significance levels). Arable weed fidelity to arable fields increases from left to right with the frequency of a species in arable fields relative to its frequency in open non-cultivated habitats. Each dot along the x-axis corresponds from left to right to the first nine deciles of the arable weed species pool ranked by increasing fidelity (e.g., the dot on the extreme right refers to the arable weed species with the highest 10% fidelity to arable fields). Regression lines were obtained by AIC selection on linear and quadratic models.

and prostrate species tolerating shade (Storkey et al., 2005; Weiner et al., 2010). Higher Ellenberg indices for nitrogen among arable weeds revealed their adaptation to the nutrient-rich environment of arable fields resulting from fertilization. Plants with low nitrogen requirements are indeed rare in arable fields (Pinke and Gunton, 2014; Wagner et al., 2017) because agricultural intensification generally selects for nitrophilous plants (Fried et al., 2009; Storkey et al., 2010; Moreau et al., 2014).

Arable weeds included 60% of therophytes, while non-weeds were mainly hemicryptophytes (65%) and geophytes (20%). This result is not surprising since the frequent disturbances occurring in arable fields, associated with tillage, herbicide application or harvest, select species avoiding unfavourable conditions (i.e., therophytes; Zanin et al., 1997; Armengot et al., 2016). Besides disturbance frequency, the timing of agricultural operations also shows great inter-annual variability resulting from the succession of crops with different sowing season (Gaba et al., 2014). Longer flowering thus confers a greater tolerance to low predictability of a favorable reproductive period. In arable fields, early and long flowering can also be interpreted as a potential strategy to escape weed control and crop competition (Bagavathiannan and Norsworthy, 2012). Arable weeds with a short or late flowering period are indeed often rare in agroecosystems (Storkey et al., 2010; Pinke and Gunton, 2014).

The functional characteristics of weeds identified here are consistent with previous studies showing that weediness is related to specific resource acquisition, growth strategies, and high tolerance to disturbances. Weeds were for example previously defined as plants with rapid growth, fast establishment of a flowering phase, continuous seed production, or tolerance to a wide range of environmental conditions (Harper, 1960; Baker, 1974; Grime, 1979), which related here to higher specific leaf area, higher proportion of therophytes, earlier and longer flowering, and larger resource requirement hypervolume. In addition, our results suggest that weediness and invasiveness may be determined by similar functional characteristics because arable weeds tend to share numerous traits

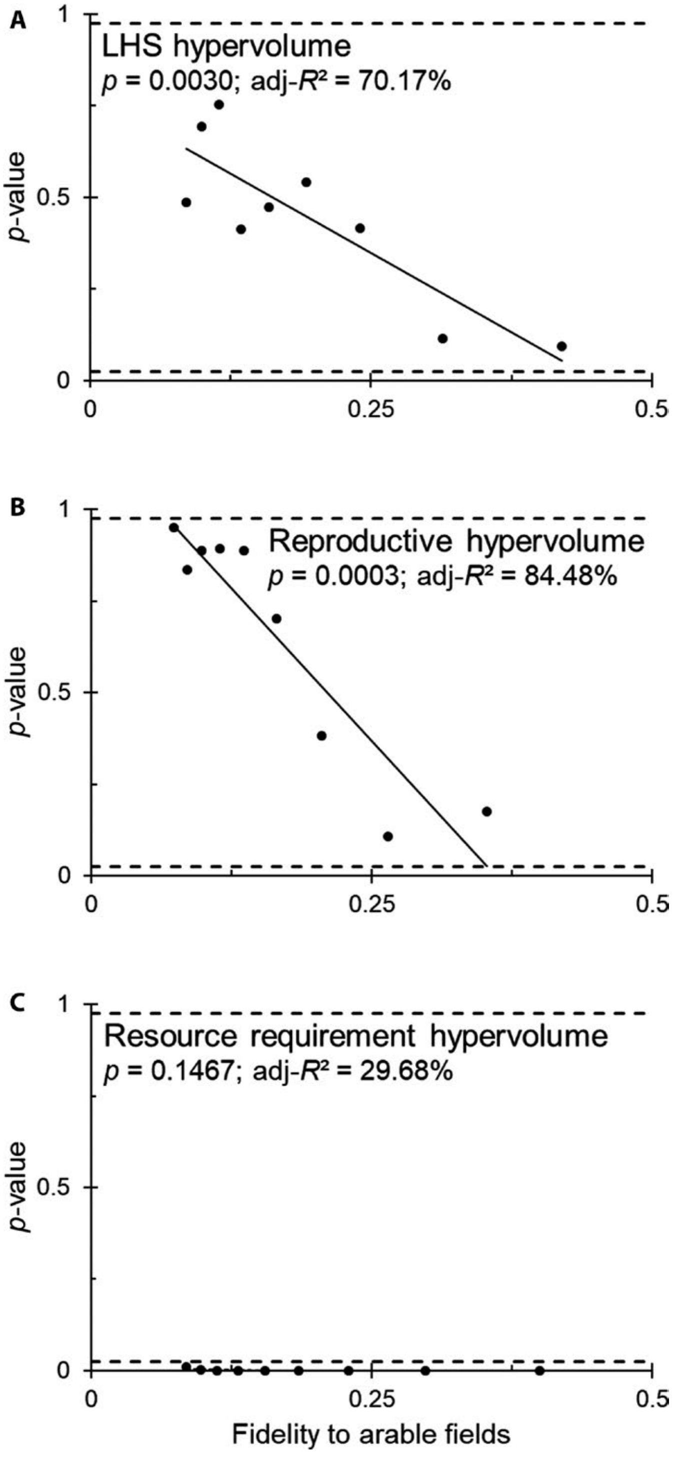

FIGURE 4. Variation in *p*-values for the volume of the hypervolume based on (A) leaf–height–seed (LHS) traits ($n = 219$ species), (B) reproductive traits ($n = 268$ species), and (C) resource requirement indices ($n = 164$ species), along a gradient of arable weed fidelity to arable fields. The *p*-values obtained through resampling correspond to the probability of the hypervolume to be significantly lower ($p \leq 0.025$) or higher ($p \geq 0.975$) than expected by chance (dotted lines show significance levels). Arable weed fidelity to arable fields increases from left to right with the frequency of a species in arable fields relative to its frequency in open non-cultivated habitats. Each dot along the *x*-axis corresponds from left to right to the first nine deciles of the arable weed species pool ranked by increasing fidelity (e.g., the dot on the extreme right refers to the arable weed species with the highest 10% fidelity to arable fields). Regression lines were obtained by AIC selection on linear and quadratic models.

with invasive alien plants. As in the arable flora studied here, weeds in the United States include more annuals than non-weeds (Kuester et al., 2014), while invasive alien plants, although called weeds in many countries, show higher photosynthetic capacity and nitrogen-use efficiency, as well as earlier and longer flowering compared to their native congeners (Pyšek and Richardson, 2007; van Kleunen et al., 2010), and generally originate from nutrient-rich productive habitats or possess large ecological niches (Dostál et al., 2013). In some respects, however, invasives are functionally distinct from natives, which may explain their absence in the arable fields sampled in the data sets investigated here. In particular, introduced weeds are generally less tolerant to shade and calcic soils compared to native ones (Kuester et al., 2014), while invasive ones often live longer and mainly propagate vegetatively compared to non-invasives (Thompson et al., 1995; Sutherland, 2004). Future studies may help to disentangle whether the absence of some invasives in arable fields predominantly relates to ecological filtering processes or to introduction history.

Arable weed functional space

The analysis of hypervolumes accounts for correlations and trade-offs among traits in functional space, which allowed us to characterize the multidimensional nature of arable weed ecological strategies and to reveal complementary insights to those of single trait comparisons. We found that arable weeds have a narrower ecological niche compared to non-weeds for both LHS and resource requirement hypervolumes. With increasing fidelity to arable fields, arable weed hypervolumes decreased, and their distance from the ones of non-weeds increased. A limited spectrum of ecological strategies thus confers arable weeds a high fidelity to arable fields. Investigating multiple functional spaces related to distinct components of plant ecological strategies (e.g., LHS, reproduction, resource requirement) further allows disentangling distinctive signatures of ecological constraints. Among the three hypervolumes investigated here, resource requirement showed the highest (and significant) functional niche breadth reduction along the fidelity gradient (80%). Indeed, when the pool of arable weeds was gradually restricted to species with higher fidelity to arable fields, affinity for nutrient-rich soils and a shady environment became more and more pronounced. While LHS and reproductive traits consistently varied with arable weed fidelity (trait variance decreased for all traits, mean flowering onset decreased, and mean SLA, flowering duration and therophyte proportion increased), these patterns did not translate into significant functional space reduction. Resource-use strategies are therefore strongly selected and determine the ability of arable weeds to persist in arable fields. Selected strategies must overcome ecological filters related to fertilization and asymmetric competition for light with crops, as already proposed (Gaba et al., 2014). Conversely, the selective pressure acting on LHS and phenological traits appeared less pronounced, thereby allowing for a broader spectrum of associated ecological strategies.

Contrary to single trait comparisons showing large differences between arable weeds and non-weeds, the analysis of hypervolumes revealed that the ecological strategies allowing species to establish in arable fields are generally diverse and often similar to plant strategies in open non-arable habitats. The use of functional spaces in combination with fidelity indices should help to identify which species can become problematic arable weeds in response to changes in agricultural practices (e.g., no-till, reduced fertilizers) among the large reservoir of species observed here, which implies important applications to forecast and manage arable weed communities. We therefore believe that multidimensional analyses should be more broadly used to complement single trait comparisons in ecological studies to better reflect the complexity of plant strategies.

Perspectives and limitations

Crop type strongly filters arable weed species, especially in relation to phenology as arable weeds generally mimic the crop species with later flowering onset and shorter flowering period in late-sowing crops (Gunton et al., 2011; Perronne et al., 2015). Such a filtering effect was not detected here because the arable weed pool was defined independently of crop types. In particular, the Biovigilance database used to calculate arable weed fidelity includes a high proportion of winter cereal fields (48%), but lower proportion of maize (21%), oilseed rape (9%) and sunflower (6%) fields, hence corresponding to the classical French crop rotation. Our results may therefore mainly reflect the ecological processes occurring under early-sowing cereal production, and additional studies are needed to investigate differences in the phenological functional space of arable weeds associated with different crop types. In addition, refining the measure of weed fidelity by accounting for the crop sequence of fields before sampling (i.e., whether an arable field sampled was cultivated as grassland—or a grassland cultivated with annual crops—in the few years before sampling) could be advisable to avoid biases in the delimitation of the species pools. More importantly, we believe that intensive efforts should be devoted in the next future to the measurement of functional traits and the completion of databases, notably for LHS traits. Indeed, for up to 42% of the arable weeds and 70% of the non-weeds in our analyses one LHS trait value was not available. Including missing trait values should not, however, greatly affect the observed functional space overlaps, as 18% of the genera missing data for at least one species included both arable weeds and non-weeds (minimum: 8.22% for flowering onset; maximum: 17.56% for SLA). A higher overlap could also be expected since only 45% of trait values (excluding biological types) are on average informed for Red-Listed arable weeds. Adding such data may therefore help understanding the decline of endangered arable weeds. Taking into account intraspecific trait variation would also be of interest, especially to test the contribution of phenotypic plasticity to fidelity to arable fields. Arable weed traits, notably leaf traits, indeed strongly vary with ontogeny and local conditions (Storkey, 2005; Perronne et al., 2014; Borgy et al., 2016).

CONCLUSIONS

Using a trait-based comparative approach, this study contributed to a better understanding of the ecological determinants of weediness; an arable weed can be defined predominantly as an early- and long-flowering therophyte with high affinity for nutrient-rich and sunny environments. Most of these characteristics of arable weeds applied also to invasive plants (Pyšek and Richardson, 2007). The original definition of arable weeds proposed here, however, mainly characterizes arable weeds with high fidelity to arable fields. Indeed, arable weeds were broadly similar to species confined to open non-arable habitats, while arable weeds with higher fidelity to arable field conditions (including some of the most harmful for crop production such as *Chenopodium album*, *Sinapis arvensis*, or *Stellaria media*) had a narrower range of functional strategies and greater functional difference. Such shrinkage of ecological niches relates principally to the constraints imposed by agricultural practices, notably heavy fertilization, frequent soil disturbances, and asymmetric competition for light. Agriculture has thus selected for specific functional strategies associated with tolerance to arable field conditions, thereby creating a pool of arable weeds by filtering out poorly adapted species. In conclusion, the pool of arable weeds is an ecologically well-defined group characterized by specific functional attributes. This large-scale study provides new insights into the functional space of arable weeds and generalizes previously observed results at a more local scale (Booth and Swanton, 2002; Navas, 2012). Such new ecological understanding will be particularly valuable for arable weed management from economic (e.g., crop yield loss; Oerke, 2006), ecological (e.g., support of ecosystem services such as pollination; Bretagnolle and Gaba, 2015), and cultural perspectives (e.g., protection of endangered species; Gerowitt et al., 2003). The determination of a trait syndrome specific to arable weeds is indeed of great interest to predict the weedy potential of newly introduced plants or of current arable weeds after changes in agricultural management.

ACKNOWLEDGEMENTS

This paper was produced with the support of CESAB-FRB as part of the activities of the DISCO-WEED Working Group. We thank Vincent Bretagnolle, Joël Chadoeuf, Christine Plumejeaud, and two anonymous reviewers for helpful comments on previous versions of the manuscript. We are very grateful to the CESAB DIVGRASS consortium for providing the grassland species list and to the French Ministry of Agriculture for providing the Biovigilance-Flore network data set. J. Storkey was supported by research programme NE/N018125/1 LTS-M ASSIST – Achieving Sustainable Agricultural Systems, funded by NERC and BBSRC (BBS/E/C/000I0120). Weed surveys in the LTSER Zone Atelier "Plaine & Val de Sèvre" were supported by the ANR Agrobiose project (grant no. ANR-13-AGRO-286 0001), the ERANET Ecodeal project (grant no. FP7 ERA-NET 691 BiodivERsA/FACCE-JPI), and the LISEA Project. C.V. was supported by the European Research Council (ERC) Starting Grant Project "Ecophysiological and biophysical constraints on domestication in crop plants" (grant ERC-StG-2014-639706-CONSTRAINTS).

AUTHOR CONTRIBUTIONS

All authors contributed ideas; F.M., G.F., C.V., and B.B. designed methodology; B.B. analyzed the data and interpreted results; and B.B. led the writing of the manuscript with F.M., S.G., and C.V. All authors contributed to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

All species lists and trait data are publicly available from published literature and the online databases Baseflor (philippe.julve.pages-perso-orange.fr), BiolFlor (biolflor.de), Ecoflora (ecoflora.org.uk) and LEDA (leda-traitbase.org).

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

APPENDIX S1. List of the 289 arable weed species investigated along the gradient of fidelity to arable fields, with noxious weeds (according to Mamarot and Rodriguez, 2011) in boldface.

APPENDIX S2. Differences in fidelity index to arable fields (mean ± SE) between arable weeds classified as noxious or non-noxious, according to Mamarot and Rodriguez (2011).

APPENDIX S3. Detailed results of χ^2 tests presented on Fig. 1. Each cell contains χ^2 component-observed number of species (expected number of species).

APPENDIX S4. Three-dimensional plots representing the arable weed (red) and non-weed hypervolumes (blue) based on (a) leaf–height–seed (LHS) traits, (b) reproductive traits, and (c) Ellenberg indices. Only one of the 1000 hypervolumes calculated by resampling is shown for arable weed species.

APPENDIX S5. Variation of mean trait along a gradient of arable weed fidelity to arable fields.

APPENDIX S6. Three-dimensional plots representing the arable weed hypervolumes based on (a) leaf–height–seed traits, (b) reproductive traits, and (c) Ellenberg indices, along a gradient of species fidelity for arable fields. Orange, red and black hypervolumes respectively, correspond to species with the highest 90%, 50% and 10% fidelity to arable fields.

APPENDIX S7. Variations in the distance between the arable weed hypervolume centroid and the non-weed hypervolume centroid based on (a) LHS traits (n = 219 species), (b) reproductive traits (n = 268 species), and (c) resource requirement indices (n = 164 species), along a gradient of arable weed fidelity to arable fields. Species fidelity for arable fields increases from left to right with the ratio of the frequency of the species in arable fields to the frequency of the species in open non-cultivated habitats. Each dot along the x-axis corresponds from left to right to the first nine deciles of the arable weed species pool ranked by increasing fidelity (e.g., the dot on the extreme right refers to arable weeds with the highest 10% fidelity to arable fields). Regression lines were obtained by AIC selection on linear and quadratic models.

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